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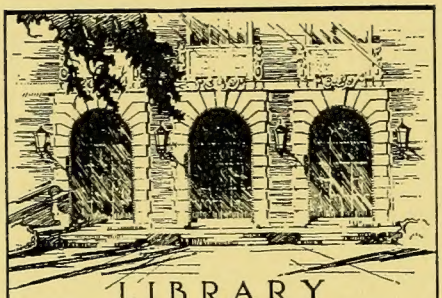

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POPULATION LOSSES IN THE MALLARD, BLACK DUCK, AND BLUE-WINGED TEAL

Frank C. Bellrose
and
Elizabeth Brown Chase

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Fig. 1.--Illinois Natural History Survey wildlife technicians banding ducks at the Chautauqua National Wildlife Refuge, north of Havana, Illinois. Banding plays an important part in most extensive studies of bird populations. More than 50,000 ducks were banded and released in Illinois in the years covered by this report. Bands were recovered from more than 10,000 of these ducks.

POPULATION LOSSES IN THE MALLARD, BLACK DUCK, AND BLUE-WINGED TEAL

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Up to about 15 years ago, few wildlife conservation agencies had a significant amount of factual information on game populations and kill. Consequently most hunting regulations governing the take of game were based largely on opinions and more often than not were applied in a hit-or-miss manner. Even though recent development of wildlife technology has given conservation agencies increasingly large amounts of factual information on which to base game regulations, most of the information obtained to the present time has been inadequate in that it has been concerned mainly with censuses of the population and inventories of the hunter take.

POPULATION MECHANICS AND MANAGEMENT

Officials engaged in drafting hunting regulations need to know more than trends in game populations and kill; they need to know the maximum proportion of a game population that can be harvested without adversely affecting the future of that population. It is evident that a large proportion of any game population will disappear each year from natural causes; it is a responsibility of management to see that the greatest possible use is made by man of the annual losses that normally occur. Shooting a wild duck in the autumn does not necessarily reduce the total spring population by one duck, for many a game bird falling before some hunter's gun would otherwise have died from natural causes before another breeding season rolled around. Paraphrased from Elton (1942): A duck shot might have died in any case the next day or week in its ordained place in the life curve.

In order to formulate the proper hunting regulations for a game species, we must first measure the total annual loss that a population of that species undergoes, and we must measure the influence of varying kill intensities on that loss. What effect does a moderate hunter-kill have on the over-all annual mortality? How high can the kill rate go in a game species before it reaches a point beyond which the productivity potential cannot bring the population back to its former level?

The year-to-year game-regulation "tactics" should come, as they often do now, from up-to-the-minute census and kill information. The population information necessary to lay out the general game-regulation "strategy" should develop from long-term band recovery data and from age ratio data. Band recoveries furnish facts on population losses; age ratios supply facts on productivity.

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ANALYSIS OF BAND DATA

The use of band data in analyses of bird populations was pioneered by Nice (1937) in her study of the song sparrow. Leopold et al. (1943) combined band and census data to determine mortality of ring-necked pheasants on the University of Wisconsin Arboretum refuge. On the other side of the Atlantic, Lack (1943a, b, c) published studies, based entirely on band recovery figures, on the survival of several English birds.

Recently Farner (1945), Buss (1946), Marshall (1947), and Hann (1948) have published on the survival and mortality of, respectively, the robin, ring-necked pheasant, herring gull, and oven-bird. Deevey (1947) presented a searching analysis and review of life tables as used to determine survival of animals in nature.

The present study deals with the survival and mortality of the mallard, black duck, and blue-winged teal in the Mississippi flyway as determined for the most part by means of 10,718 recoveries (bands recovered from ducks shot and bagged or ducks found dead) from 51,297 individuals banded by the Natural History Survey at the Chautauqua National Wildlife Refuge, near Havana, Illinois, fig. 1, or at McGinnis Slough, in and with the co-operation of the Forest Preserve District of Cook County, near Orland Park, Illinois. The actual banding was done during the fall months, 1939-1944, at Lake Chautauqua and, 1940-1945, at McGinnis Slough; recovery data extend through 1946 for Lake Chautauqua and 1947 for McGinnis Slough. Inclusion of the McGinnis Slough data in this report was made possible through the co-operation of Roberts Mann, Dr. David H. Thompson, and John Jedlicka.

VALIDITY OF SHOT RECOVERIES.--Previous investigations indicate that satisfactory appraisals of longevity can be made from band recoveries of shot birds. Paynter (1947) found that there was no significant difference in mean length of life between herring gulls dying as a result of shooting, trapping, or other human interference and those dying as a result of natural or unknown causes. Farner (1945) showed that, in robins, life-expectancy figures obtained from the number of birds shot and from the number killed by cats were similar to those calculated from band recoveries representing the total population.

Band recoveries from shot ducks are many times as numerous as records of live recaptures or other returns, and they provide the largest sampling on which to base life tables.

The number of band recoveries from ducks in a banding-class* shot in a particular year following banding is dependent on two principal factors: (1) the number of ducks in the banding-class left alive to be bagged and (2) the shooting pressure. If shooting pressure in two specified years is equal, then the difference in the number of band recoveries in the two years would be a measure of total population loss from the first year to that following. However, there has been a year-to-year variation in shooting pressures. In Chautauqua-banded mallards the season-of-banding bag ranged from 6.7 to 14.9 per cent of birds banded, 1939-1944, table 9. This year-to-year variation results in a sampling error when the population loss is measured for any specified year considered separately. But because ducks of most

* Banding-class refers to the ducks banded in a specified year.

year-classes* are represented in several calendar years, the year-to-year variation in recovery data resulting from changes in shooting pressure has been minimized for each year-class but that for 7-8, table 1.

After analyzing figures obtained from banded mallards that return to the traps in subsequent years, we have concluded that these data do not allow for a valid interpretation of population losses because of the small size of the sample and because of yearly variations in rate of return of ducks to the same flyway resting or feeding grounds. Our band returns show that, although in each year there is some degree of return by mallards to the same flyway rest stops, the degree of return varies from year to year.

Because band recoveries from shot ducks representing the extensive areas over which ducks fly are not only many times as numerous as records of live recaptures but are not subject to yearly variations in the return to a single spot on the flyway, these band recoveries were used in this study to measure population losses in the mallard, black duck, and blue-winged teal.

YEAR-OF-BANDING RECOVERY CORRECTIONS.--In order to use recovery data obtained the same year that mallards and black ducks were banded, we found it necessary to compensate for the fact that banding was done south of the breeding grounds during the hunting season rather than on the breeding grounds immediately preceding the hunting season. To correct for the chronological and geographical differences involving band recoveries in the season of banding (part of hunting season and south half of flyway) and band recoveries in subsequent seasons (entire hunting season and entire flyway), we used a simple ratio that involved the number of days banded ducks were actually available for shooting and the number of days these banded ducks would have been available if all had been banded before the beginning of the season. Corrections were made separately for each calendar year and for each age and sex group.

The first step in making the corrections in year-of-banding data involved finding the number of ducks banded in each autumn banding period and then locating for each period the mean date of banding activities. This mean date assumes that all ducks were banded on a single day a definite length of time after banding was begun and before it was ended. The next step was to determine the number of days from the mean banding date to the end of banding.

The daily rate of mallard kill was found to be approximately the same before and after the mean banding date. This rate of kill was determined by tabulating returns through the hunting season for mallards banded at least one year previously. Very few mallards were killed in September, more in October, and most in November; then the kill declined through December. So that the data would more nearly resemble a normal curve, the number killed in September was added to the number for October, and October 1 was assumed in calculations to be the first day of banding.

* The ducks in a year-class are those killed in the year of banding or in a specified number of years after being banded and are indicated in table 1 by the columns headed O-1 corrected, 1-2, 2-3, etc. Ducks in year-class 1-2 are those killed during the period between 1 and 2 years after being banded.

The formula for deriving the corrected number of recoveries for the O-1 year-class to the end of the banding period is as follows:

$$\frac{\text{Corrected number of recoveries from October 1 to end of banding period}}{\text{Actual number of recoveries before end of banding period}} = \frac{\text{Number of days from October 1 to end of banding period}}{\text{Number of days from mean banding date to end of banding period}}$$

Recoveries from the time banding is terminated until September 1 of the following year are added to the corrected number of bands recovered up to the end of the banding period. The result gives the corrected year-of-banding recovery data, which are roughly comparable to recovery data for ducks banded on the breeding grounds before the beginning of the hunting season.

Below is given an example of the use of the formula in correcting the year-of-banding recovery data. Bands were recovered from 33 juvenile male mallards during the 1939 banding period and 16 after the end of this period but before the following September 1 -- a total of 49 recoveries, table 1. The number of days from October 1 to termination of banding in 1939 was 89. The number of days from mean banding date to end of the banding period was 28.2.

Substituting the appropriate figures in the formula gives the following equation:

$$\frac{x}{33} = \frac{89}{28.2}$$

$$x = \frac{89 \times 33}{28.2}$$

$$x = 104$$

To 104, the corrected number of band recoveries before the end of the banding period, are added the 16 recoveries after the end of this period, to give a total of 120, table 1.

Another method by which the corrected number of recoveries can be determined is more nearly accurate for individual years, but it requires a good sample of recoveries for a given year from prior bandings; it cannot be used for the year in which banding is first instituted.

This formula is as follows:

$$\frac{\text{Corrected number of recoveries from selected year of banding}}{\text{Actual number of recoveries from selected year of banding before end of banding period}} = \frac{\text{Total number of previously banded ducks recovered in selected year}}{\text{Number of previously banded ducks recovered after mean selected-year banding date before end of banding period}}$$

In addition to these two formulas developed by the authors for correcting current-year banding data on the flyways is still a third method, which was developed simultaneously and independently by Thompson & Jedlicka (1948).

Year-of-banding band recoveries for the blue-winged teal, table 7, were not corrected

as were year-of-banding mallard and black duck recoveries, because most of the blue-wings were banded before the hunting season opened.

LIFE TABLES AND TERMINOLOGY.--In the life tables presented here, mortality figures and survival figures were derived from figures representing the number of bands recovered and the number of ducks banded in each of the various year-classes. Returns are complete for the first three year-classes; so the percentage of return is based on the total number of ducks banded, tables 1-7. For the fourth year-class (3-4), returns are lacking for 1 year (banding-class); so only the number of birds banded prior to that year are considered. Each succeeding year-class has returns for 1 year less; the 7-8 year-class has returns for only 1 year.

In the mortality* series, the percentage of the total number of bands recovered is given for each year-class, tables 1-7. The figure for any one year-class represents a percentage of the total number of recoveries.

The cumulative per cent of bands recovered, as presented in tables 1-7, is found for any one year-class by adding the mortality series figure for that year-class to the mortality series figures for all previous year-classes. Figures in the survival series, the reverse of the mortality series, are obtained for any one year-class by subtracting from 100 the number representing the cumulative per cent of bands recovered for that year-class. The mortality rate, which measures the percentage of those birds alive at the start of a year that die in that year, is found for any year-class by dividing the mortality series figure for that year-class by the survival series figure for the previous year-class; for year-class O-1, the survival series figure for the previous year-class is 100 per cent.

POPULATION LOSSES.--Mortality and survival figures of a population of ducks of known age are given in table 1. Banded as juveniles, the mallard drakes making up this population probably ranged in age from 3 to 7 months at time of banding at Lake Chautauqua.

Data in table 1 indicate that in this population of mallards banded as juveniles, and therefore of known age throughout their history, for every 100 alive on October 1 of the year of banding 55 (54.9 per cent) died before the next October 1. In the second year following banding, 20 additional ducks died; in the third year 11; in the fourth year 6. By the end of the sixth year, only 2 (1.9 per cent) were still alive.

Mortality and survival figures for a population of mallard drakes banded as adults are given in table 2. The ages of the individuals were unknown except that all were at least a few months more than 1 year of age at the time of banding. Data in the table indicate that for every 100 of these mallard drakes alive on October 1 of the year of banding 36 died before October 1 of the following year; 25 died the second year, 15 the third year, and 11 (10.5 per cent) the fourth year. By the end of the sixth year less than 3 (2.5 per cent) were still alive.

The principal difference in the mortality rates of the two groups of ducks, one banded as juveniles and the other banded as adults, was in the greater year-of-banding losses in

* The term mortality as used in this paper includes death caused by hunters and by natural forces; it is applied only to ducks that have reached flying stage.

Table 1.--Mortality and survival of male mallards banded as juveniles at Lake Chautauqua, 1939-1944. Figures based upon bands recovered up to January 1, 1947, from birds shot or found dead.

Year Banded	Total Banded	Recoveries in Years Following Banding (Sept. 1 - Aug. 31)									
		O-1 Uncorrected	O-1 Corrected*	1-2	2-3	3-4	4-5	5-6	6-7	7-8	Total
1939	1,088	49	120	54	30	17	8	9	6	2	246
1940	1,615	200	391	116	54	18	24	13	10		626
1941	1,090	43	98	89	35	28	13	9			272
1942	1,717	177	342	80	51	37	17				527
1943	1,892	146	272	111	86	27					496
1944	617	56	138	41	15						194
Grand total	8,019	671	1,361 of 8,019 banded	491 of 8,019 banded	271 of 8,019 banded	127 of 7,402 banded	62 of 5,510 banded	31 of 3,793 banded	16 of 2,703 banded	2 of 1,088 banded	2,361
Per cent of bands recovered			16.97	6.12	3.38	1.72	1.12	0.82	0.59	0.18	30.90
Mortality series, or per cent of total number of bands recovered in each year-class			54.9	19.8	10.9	5.6	3.7	2.6	1.9	0.6	100.00
Cumulative per cent of bands recovered			54.9	74.7	85.6	91.2	94.9	97.5	99.4	100.0	
Survival series, or per cent of total number of banded ducks in each year-class alive at end of year			45.1	25.3	14.4	8.8	5.1	2.5	0.6	0.0	
Mortality rate, or per cent of banded ducks in each year-class alive at beginning of year lost during year+			54.9	43.9	43.1	38.9	42.0				

*Corrected figures derived as explained on pages 5 and 6 of text. +Average 44.56 per cent.

Table 2.--Mortality and survival of male mallards banded as adults at Lake Chautauqua, 1939-1944. Figures based upon bands recovered up to January 1, 1947, from birds shot or found dead.

Year Banded	Total Banded	Recoveries in Years Following Banding (Sept. 1 - Aug. 31)									
		O-1 Uncorrected	O-1 Corrected*	1-2	2-3	3-4	4-5	5-6	6-7	7-8	Total
1939	1,486	65	123	82	51	48	16	15	9	1	345
1940	2,647	132	268	166	114	58	55	28	17		706
1941	2,110	57	130	138	57	57	35	34			451.
1942	3,142	216	339	155	114	82	39				729
1943	2,763	138	232	190	115	72					609
1944	2,117	125	185	149	71						405
Grand total	14,265	733	1,277 of 14,265 banded	880 of 14,265 banded	522 of 14,265 banded	317 of 12,148 banded	145 of 9,385 banded	77 of 6,243 banded	26 of 4,133 banded	1 of 1,486 banded	3,245
Per cent of bands recovered			8.95	6.17	3.66	2.61	1.54	1.23	0.63	0.07	24.86
Mortality series, or per cent of total number of bands recovered in each year-class			36.0	24.8	14.7	10.5	6.2	5.0	2.5	0.3	100.00
Cumulative per cent of bands recovered			36.0	60.8	75.5	86.0	92.2	97.2	99.7	100.00	
Survival series, or per cent of total number of banded ducks in each year-class alive at end of year			64.0	39.2	24.5	14.0	7.8	2.8	0.3	0.00	
Mortality rate, or per cent of banded ducks in each year-class alive at beginning of year lost during year+			36.0	38.8	37.6	42.9	44.5				

*Corrected figures derived as explained on pages 5 and 6 of text. +Average 39.96 per cent.

Table 3.--Mortality and survival of all male mallards banded at Lake Chautauqua, 1939-1944. Figures based upon bands recovered up to January 1, 1947, from birds shot or found dead.

Year Banded	Total Banded	Recoveries in Years Following Banding (Sept. 1 - Aug. 31)									
		O-1 Uncorrected	O-1 Corrected*	1-2	2-3	3-4	4-5	5-6	6-7	7-8	Total
1939	2,574	114	243	136	81	65	24	24	15	3	591
1940	4,262	332	659	282	168	76	79	41	27		1,332
1941	3,200	100	228	227	92	85	48	43			723
1942	4,859	393	681	235	165	119	56				1,256
1943	4,655	284	504	301	201	99					1,105
1944	2,734	181	323	190	86						599
Grand total	22,284	1,404	2,638 of 22,284 banded	1,371 of 22,284 banded	793 of 22,284 banded	444 of 19,550 banded	207 of 14,895 banded	108 of 10,036 banded	42 of 6,836 banded	3 of 2,574 banded	5,606
Per cent of bands recovered			11.84	6.15	3.56	2.27	1.39	1.08	0.61	0.12	27.02
Mortality series, or per cent of total number of bands recovered in each year-class			43.8	22.8	13.2	8.4	5.1	4.0	2.3	0.4	100.0
Cumulative per cent of bands recovered			43.8	66.6	79.8	88.2	93.3	97.3	99.6	100.0	
Survival series, or per cent of total number of banded ducks in each year-class alive at end of year			56.2	33.4	20.2	11.8	6.7	2.7	0.4	0.0	
Mortality rate, or per cent of banded ducks in each year-class alive at beginning of year lost during year+			43.8	40.6	39.4	41.6	43.5				

*Corrected figures derived as explained on pages 5 and 6 of text. +Average 41.78 per cent.

Table 4.--Mortality and survival of all female mallards banded at Lake Chautauqua, 1939-1944. Figures based upon bands recovered up to January 1, 1947, from birds shot or found dead.

Year Banded	Total Banded	Recoveries in Years Following Banding (Sept. 1 - Aug. 31)									
		0-1 Uncorrected	0-1 Corrected*	1-2	2-3	3-4	4-5	5-6	6-7	7-8	Total
1939	900	28	56	58	24	15	5	6	3	2	169
1940	1,578	110	214	85	39	23	16	5	2		384
1941	1,634	43	96	98	39	25	25	6			289
1942	1,995	119	189	94	46	19	8				356
1943	1,790	90	159	77	42	19					297
1944	731	41	61	34	19						114
Grand total	8,628	431	775 of 8,628 banded	446 of 8,628 banded	209 of 8,628 banded	101 of 7,897 banded	54 of 6,107 banded	17 of 4,112 banded	5 of 2,478 banded	2 of 900 banded	1,609
Per cent of bands recovered			8.98	5.17	2.42	1.28	0.89	0.41	0.20	0.22	19.57
Mortality series, or per cent of total number of bands recovered in each year-class			45.9	26.4	12.4	6.5	4.5	2.1	1.1	1.1	100.0
Cumulative per cent of bands recovered			45.9	72.3	84.7	91.2	95.7	97.8	98.9	100.0	
Survival series, or per cent of total number of banded ducks in each year-class alive at end of year			54.1	27.7	15.3	8.8	4.3	2.2	1.1	0.0	
Mortality rate, or per cent of banded ducks in each year-class alive at beginning of year lost during year+			45.9	48.8	44.7	42.6	51.4				

*Corrected figures derived as explained on pages 5 and 6 of text. +Average 46.68 per cent.

Table 5.--Mortality and survival of all mallards banded at McGinnis Slough, 1940-1945. Figures based upon bands recovered up to January 1, 1948, from birds shot or found dead.

Year Banded	Total Banded	Recoveries in Years Following Banding (Sept. 1 - Aug. 31)									
		O-1 Uncorrected	O-1 Corrected*	1-2	2-3	3-4	4-5	5-6	6-7	7-8	Total
1940	483	27		20	20	6	4	6	2	0	
1941	312	21		22	10	2	1	5	1		
1942	1,882	143		86	56	32	17	6	0		
1943	3,009	138		212	125	54	24	2			
1944	1,778	168		121	56	22	1				
1945	2,287	170		154	61						
Grand total	9,751	667	1,127 of 9,751 banded	615 of 9,751 banded	328 of 9,751 banded	116 of 7,464 banded	49 of 5,686 banded	19 of 2,677 banded	3 of 795 banded		2,257
Per cent of bands recovered			11.48	6.30	3.36	1.55	0.86	0.70	0.39		24.64
Mortality series, or per cent of total number of bands recovered in each year-class			46.6	25.6	13.6	6.3	3.5	2.8	1.6		100.0
Cumulative per cent of bands recovered			46.6	72.2	85.8	92.1	95.6	98.4	100.0		
Survival series, or per cent of total number of banded ducks in each year-class alive at end of year			53.4	27.8	14.2	7.9	4.4	1.6	0.0		
Mortality rate, or per cent of banded ducks in each year-class alive at beginning of year lost during year+			46.6	47.9	48.9	44.4	44.3				

*Corrected figures derived from Thompson & Jedlicka (1948). +Average 46.42 per cent.

Table 6.--Mortality and survival of all black ducks banded at McGinnis Slough, 1940-1945. Figures based upon band recoveries up to January 1, 1948, from birds shot or found dead.

Year Banded	Total Banded	Recoveries in Years Following Banding (Sept. 1 - Aug. 31)									
		O-1 Uncorrected	O-1 Corrected*	1-2	2-3	3-4	4-5	5-6	6-7	7-8	Total
1940	123	12	15	8	7	1	2	0	0	0	33
1941	659	38	47	44	20	13	12	3	1		140
1942	1,069	91	134	51	33	10	6	3			237
1943	962	44	63	72	24	24	4				187
1944	852	93	144	31	22	12					209
1945	716	54	67	49	17						133
Grand total	4,382	332 of 4,382 banded	470 of 4,382 banded	255 of 4,382 banded	123 of 4,382 banded	60 of 3,665 banded	24 of 2,813 banded	6 of 1,851 banded	1 of 782 banded		939
Per cent of bands recovered			10.72	5.82	2.81	1.64	0.85	0.32	0.13		22.29
Mortality series, or per cent of total number of bands recovered in each year-class			48.1	26.1	12.6	7.4	3.8	1.4	0.6		100.0
Cumulative per cent of bands recovered			48.1	74.2	86.8	94.2	98.0	99.4	100.0		
Survival series, or per cent of total number of banded ducks in each year-class alive at end of year			51.9	25.8	13.2	5.8	2.0	0.6			
Mortality rate, or per cent of banded ducks alive at beginning of year lost during year+			48.1	50.3	48.8	56.0	65.5				

*Corrected figures derived as explained on pages 5 and 6 of text.

+Average 53.74 per cent.

Table 7.--Mortality and survival of all blue-winged teals banded at McGinnis Slough, 1940-1945. Figures based upon band recoveries up to January 1, 1948, from birds shot or found dead.

Year Banded	Total Banded	Recoveries in Years Following Banding (Sept. 1 - Aug. 31)							
		0-1	1-2	2-3	3-4	4-5	5-6	6-7	Total
1940	137	3	3	1	1	0	0	0	8
1941	1,233	17	12	13	4	3	0	0	49
1942	1,343	37	17	6	4	1	2		67
1943	976	18	18	9	2	1			48
1944	1,498	54	26	4	4				88
1945	1,065	31	9	7					47
Grand total	6,252	160 of 6,252 banded	85 of 6,252 banded	40 of 6,252 banded	15 of 5,187 banded	5 of 3,689 banded	2 of 2,713 banded		307
Per cent of bands recovered-----		2.55	1.36	0.64	0.29	0.14	0.07		5.05
Mortality series, or per cent of total number of bands recovered in each year-class ----------		50.5	26.9	12.7	5.7	2.8	1.4		100.00
Cumulative per cent of bands recovered----------		50.5	77.4	90.1	95.8	98.6	100.0		
Survival series, or per cent of total number of banded ducks in each year-class alive at end of year----------		49.5	22.6	9.9	4.2	1.4	0.0		
Mortality rate, or per cent of banded ducks alive at beginning of year lost during year* ---		50.5	54.3	56.2	57.6	66.7			

*Average 57.06 per cent.

the ducks banded as juveniles, tables 1 and 2. A comparison of mortality rates of the two groups discloses that in the first 4 years after the year of banding the average yearly rate of loss was 42 per cent in the group banded as juveniles (average of 43.9, 43.1, 38.9, and 42.0), and 41 per cent in the group banded as adults (average of 38.8, 37.6, 42.9, and 44.5). The significant fact these figures reveal is that senescence is not an important mortality factor in wild mallard populations. Shooting, accidents, and predation are responsible for most of the deaths, and juveniles are more subject to these causes of mortality than are older ducks.

The higher year-of-banding mortality rate in juvenile populations is partly, but not entirely, the result of a higher proportion of juveniles taken by hunters. The mortality rate is about 1-1/2 times as high for juveniles as for adults, tables 1 and 2, and the hunting vulnerability* rate is approximately in the same proportion. Differences in the survival rates of mallard drakes banded as adults and those banded as juveniles are presented graphically in fig. 2.

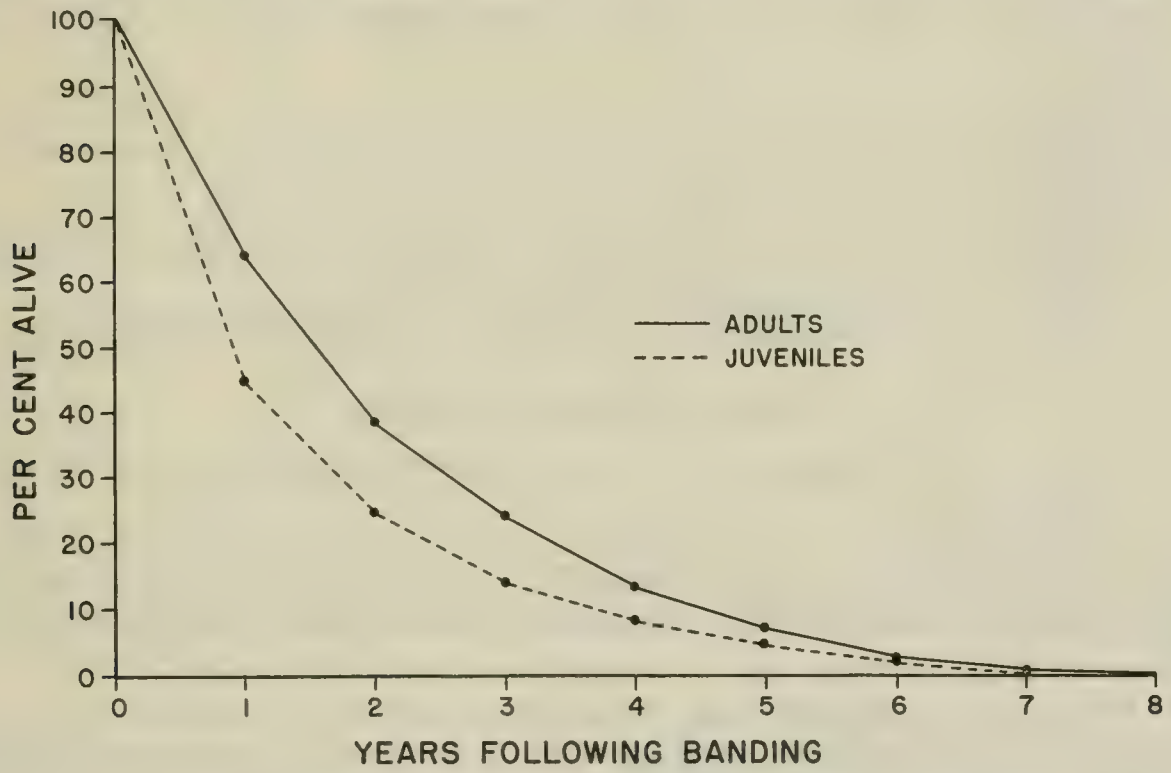

Fig. 2.--Survival rates of mallard drakes banded at Lake Chautauqua, 1939-1944, one group banded as adults and the other banded as juveniles.

There was a higher rate of loss among mallard hens than among mallard drakes, as shown by differences in the mortality rates, tables 3 and 4. This loss in hens occurred despite the fact that current-season or year-class O-1 band data derived from figures in tables 3 and 4 show that drakes in this year-class are 4 per cent more vulnerable to hunting than are hens. It would appear, then, that the greater hen mortality occurs outside of the hunting season. Field studies indicate that hens during the breeding season are subject to more hazards than

* The term vulnerability in this paper refers to the deaths of birds bagged by hunters, whereas mortality refers to deaths from all causes, including deaths resulting from crippling by hunters.

are males. While the hens, incubating their eggs and caring for their young, are subject to high mortality, the drakes gather in bands in large marshes or on extensive lakes where such decimating factors as predation and drought apparently cause fewer losses. Differences in the survival rates of mallard drakes and hens are presented graphically in fig. 3.

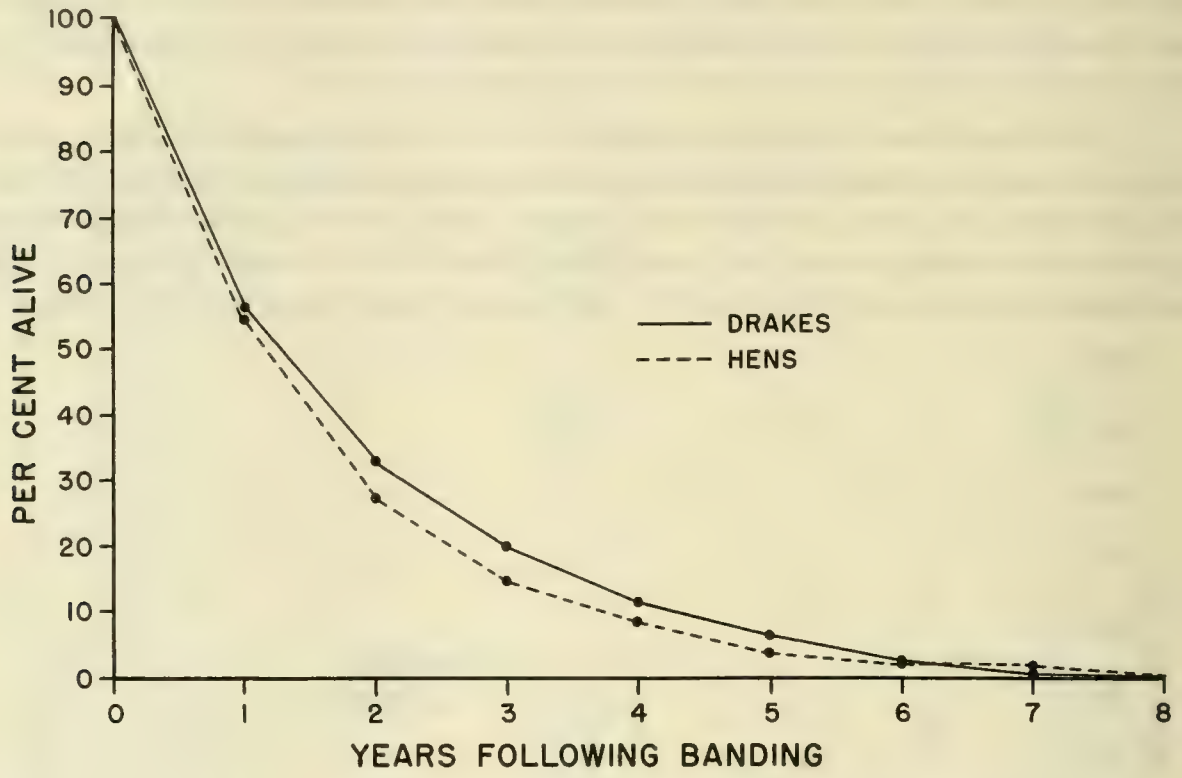

Fig. 3.--Survival rates of mallard drakes and mallard hens banded at Lake Chautauqua, 1939-1944.

Banding traps are selective in that in most situations they take a disproportionate number of individuals in one or more of the various age and sex groups (usually the adult male group). Therefore, life tables based on banding data in which figures for all age and sex groups are lumped together usually are not representative of the population involved.

However, at McGinnis Slough, trap selectivity was at a minimum because a relatively low population density allowed the ducks there to feed into the traps in such a way that seldom did an age or sex group dominate the situation, and the trapped population was fairly representative of the population using the area. Because of this relative lack of selectivity in trapping and because the number of ducks involved was small, the data on all age and sex groups of each of the three species treated in this paper have been combined in determining mortality losses, tables 5, 6, and 7.

Among McGinnis Slough mallards, the mortality losses for all age and sex groups, table 5, approximated losses suffered by mallard hens banded at Lake Chautauqua, table 4, and were slightly higher than mortality losses suffered by the entire mallard group banded at Lake Chautauqua.

Black ducks banded at McGinnis Slough, table 6, had mortality losses that totaled 94.2 per cent through year-class 3-4, while mallards banded there had losses amounting to 92.1 per cent through the same year-class. The average of yearly mortality rates through year-class 4-5 was 53.7 per cent for the black duck, 46.4 per cent for the mallard.

Blue-winged teals banded at McGinnis Slough, table 7, had higher mortality losses than either mallards or black ducks banded there. The average of yearly mortality rates for the blue-wings was 57.1 per cent, more than 3 per cent higher than for black ducks. Although there was no well-defined yearly trend in the mortality rates of the mallards and black ducks, the mortality rate of the blue-winged teals increased with each successive year-class.

LONGEVITY.--Longevity, as used here, is the life expectancy of a duck after banding. Longevity research does not provide information essential for evaluating population mechanics, but it may provide figures readily comprehended by the layman. Because some investigators have used them, we include longevity figures for mallards for comparison with the figures for other species.

There is a difference in longevity data as obtained by mean (average) and by median (mid-point) figures, table 8. This difference occurs because a few individuals lived a disproportionately large number of years. Because the median figures are more precise measurements of population longevity, we believe they should be used in measurements of longevity, particularly in comparisons with other species.

Table 8.--Expectation of further life after September 1 in year of banding by mallards banded at Lake Chautauqua, 1939-1944, as determined from mean and median calculations.

Statistic Used	Life Expectancy in Years			
	Adult Male	Juvenile Male	Adult Male and Juvenile Male	Female
Mean (average)	1.79	1.27	1.56	1.38
Median (mid-point)	1.04	0.23	0.52	0.41

According to figures presented by Addy (1945) the longevity of the black duck in New England is slightly less than that of the mallard in Illinois. Addy found that the average life span of black ducks after banding at three stations in Massachusetts was 1.17, 1.29, and 1.49 years. In Illinois the life span of mallard drakes averaged 1.56 years and that of hens 1.38 years in the years of this study.

YEARLY HUNTER-BAG. --Yearly hunter-bag losses for mallards are given in tables 9 and 10, for black ducks in table 11, and for blue-winged teals in table 12. These bag figures involve only those ducks from which the bands were recovered in the year of banding. In the case of mallards and black ducks, the figures are corrected to compensate for banding during the hunting season mid-way down the flyway.

Table 9.--Per cent of mallards banded at Lake Chautauqua, 1939-1944, bagged in year of banding, as determined by band recoveries.

Year of Banding	Number of Mallards Banded	Per Cent of Banded Mallards Bagged in Year of Banding*
1939	3,474	8.6
1940	5,840	14.9
1941	4,834	6.7
1942	6,854	12.6
1943	6,445	10.2
1944	3,465	11.1

*Corrected to compensate for time and place of banding: during the hunting season and halfway down the flyway. Not corrected to compensate for bands not reported.

Of particular note is the finding that yearly variations in rate of mallard loss were somewhat similar at the two banding stations, about 175 miles apart. There was also similarity in trends in the year-to-year percentage losses in the mallard, the black duck, and even in the early migrating blue-winged teal.

The lowest rates of hunter-bag losses in mallards occurred in 1939, 1941, 1943, and 1947. The highest were in 1940, 1942, 1944, 1945, and 1946. The bag in the period 1944-1947 averaged about 1.5 per cent more per year than it did in the period 1940-1943.

Table 10.--Per cent of mallards banded at McGinnis Slough, 1940-1947, bagged in year of banding, as determined by band recoveries.

Year of Banding	Number of Mallards Banded	Per Cent of Banded Mallards Bagged in Year of Banding*
1940	483	13.7
1941	312	8.3
1942	1,882	13.3
1943	3,009	8.8
1944	1,778	15.7
1945	2,287	14.7
1946	1,634	12.9
1947	973	6.2

*Corrected to compensate for time and place of banding: during the hunting season and halfway down the flyway. Not corrected to compensate for bands not reported.

Table 11.--Per cent of black ducks banded at McGinnis Slough, 1940-1945, bagged in year of banding, as determined by band recoveries.

Year of Banding	Number of Black Ducks Banded	Per Cent of Black Ducks Bagged in Year of Banding*
1940	123	12.2
1941	659	7.1
1942	1,069	12.5
1943	962	6.5
1944	852	16.9
1945	716	9.4

*Corrected to compensate for time and place of banding: during the hunting season and halfway down the flyway. Not corrected to compensate for bands not reported.

Table 12.--Per cent of blue-winged teals banded at McGinnis Slough, 1940-1945, bagged in year of banding, as determined by band recoveries.

Year of Banding	Number of Blue-Wings Banded	Per Cent of Banded Blue-Wings Bagged in Year of Banding*
1940	137	2.2
1941	1,233	1.4
1942	1,343	2.8
1943	976	1.8
1944	1,498	3.6
1945	1,065	2.9

*Not corrected to compensate for bands not reported.

EVALUATION OF POPULATION SURVIVAL AND LOSSES

Available records show that birds live longer in captivity than in the wild state. Flower (1926) reported that the length of life of 20 pintails and widgeons in aviaries was 21 years and 5 months, and 5 of the 20 were still alive at the time of his report. Jean Delacour of the American Museum of Natural History (letter, February, 1947) stated that in a well-run aviary there is a yearly loss of 5 per cent of the ducks from illness and another 5 per cent from accidents. The larger species of ducks begin to show signs of old age at 20 years. In the wild, decimating factors are so great that few ducks ever reach senescence. From the tens of thousands of wild mallards banded, Cooke (1942, 1943) listed the length of life of the four individuals living the longest from banding to reported death as 8, 8, 10, and 14 years.

Do Mississippi flyway mallards and black ducks lead a more hazardous life than other birds? Mortality rates for several species recently studied are given in table 13. It is evident

Table 13.--Mortality rates for various bird populations as determined by recent studies.

Bird Population	Mortality Rate, Per Cent			Source**
	Year of Banding	Subsequent Years	All Years	
Mallard (Chautauqua)*	55	39-44	--	Table 1
Mallard (McGinnis)+	--	--	44-49	Table 5
Mallard (England)	88	65	--	Hohn (1948)
Black duck (McGinnis)	--	--	48-66	Table 6
Blue-winged teal (McGinnis)	--	--	51-67	Table 7
Canada goose	74	56-66	--	Hanson & Smith (1950)
Ruffed grouse	--	--	50-58	Bump et al. (1947)
Ring-necked pheasant	70	70	--	Leopold et al. (1943)
Ring-necked pheasant	74-81	56-65	--	Buss (1946)
Herring gull	60	29-48	--	Marshall (1947)
Robin	53	53	--	Farner (1945)
Oven-bird	45	46	--	Hann (1948)

*Juvenile males. +All ages and sexes. **Tables referred to are those in this paper.

that these mallards and black ducks, even though experiencing heavy shooting pressure, do not suffer from exceptionally high mortality rates, for the mortality rates are lower than for some other game birds and not much higher than for the protected herring gull, the robin, or the oven-bird. Mallards studied by Hohn (1948) in England had a much higher mortality rate than that found in the present study for North American mallards. The year-of-banding mortality rate of 88 per cent in mallards banded as young in England was three-fifths greater than that of male mallards banded as juveniles at Lake Chautauqua. The mortality rate among adult-banded mallards the year of banding in England was two-thirds greater than the mortality rate among adult-banded male mallards the year of banding at Lake Chautauqua.

It is well recognized that blue-winged teals do not suffer as heavy hunting losses as do Mississippi flyway mallards. Hunting seasons open so late in the United States that most of these teals have departed for southern regions by the opening dates. Yet despite low gunning losses, table 12, the blue-winged teal had higher annual mortality losses than the mallard. Ring-necked pheasants (Leopold et al. 1943, Buss 1946) that were fully or partially protected from hunting had a higher mortality rate than shot mallard populations, table 13. Canada geese in the Horseshoe Lake region of southern Illinois, 1940-1947, underwent higher losses than did Chautauqua-banded mallards (Hanson & Smith 1950). However, this goose population was so heavily shot that it was undergoing a decline at the time measurements were taken.

The ruffed grouse survival rate from one September to the next averaged 49.8 per cent, 1930-1941, at the Connecticut Hill study area and 42.1 per cent, 1931-1941, at the Adirondack study area (Bump et al. 1947). Mallard males banded as juveniles at Lake Chautauqua had a first-year survival rate of 45 per cent and a subsequent-year survival rate for the next 4 years of 56 to 61 per cent. Mallards of all ages and of all year-classes banded at McGinnis Slough had a yearly survival rate of 51 to 56 per cent the first 5 years after banding.

NATURAL VERSUS SHOOTING LOSSES.--Shooting losses as measured by band recoveries reported from shot ducks furnish worthwhile figures on year-to-year hunting bags, but additional information is needed before these losses can be used as a measure of the total mortality caused by hunting.

It is evident that a large number of hunters shooting banded ducks fail to report the bands. At the time he wrote, McIlhenny (1934) believed that "fully 50 per cent" of the banded ducks shot were reported. Leopold (1933) polled a number of game managers and officials as to their estimate of the percentage of banded ducks taken but not reported; the estimates were as follows: the Carolinas, 80 per cent; Connecticut, 50 per cent; Memphis area (at clubs) 5 per cent, (elsewhere) 10 per cent; Arkansas, 60 per cent. A questionnaire study made in Illinois (Bellrose 1945) indicated that about 25 per cent of the duck bands taken in the state were not reported.

During the 1948 hunting season the United States Fish and Wildlife Service issued special "reward" bands. These bands, issued for use on mallards and black ducks, were similar to other bands except that they carried a notation of a reward if sent to the Service. We placed 200 "reward" bands alternately with 242 other bands on 442 mallards at the Spring Lake Wildlife Refuge, Savanna, Illinois, during late October and early November, 1948. Of 71 returns received up to May 1, 1949, 50 were from reward bands. Reward bands were reported about 2.9 times as frequently in proportion to the numbers applied as were non-reward bands.

Probably not all reward bands taken from shot ducks were reported. However, since the reward bands provide the most nearly accurate figure yet available relative to bands reported by hunters, we have used this figure as a correcting factor in some of our calculations.

Year-of-banding recoveries, corrected for banding during the hunting season, from Illinois-banded mallards ranged from 6 to 16 per cent, tables 9 and 10, and averaged about 11 per cent. Allowing an additional 190 per cent for bands from mallards bagged but not reported would raise the proportion of the mallard population taken home by hunters to about 32 per cent. It should be kept in mind that this correction is based on the 442 birds banded at Savanna, Illinois, and not on the complete recovery list of reward bands issued by the Fish and Wildlife Service to all co-operators.

Losses through crippling are an additional shooting drain that must be reckoned with. Records obtained from interviewing hunters at clubs and public shooting grounds in Illinois, table 14, show a crippling loss that ranges between 18 and 41 per cent of the ducks bagged, depending upon the type of shooting. An over-all appraisal of hunters' reports indicates that in

Illinois the knocked-down cripple loss is about 30 per cent of the number of ducks bagged, or about 9 per cent of the total population. It is known that at least a small proportion of these cripples recover; it is also known that, of the ducks shot at but apparently unharmed, many are

Table 14.--Ratio of cripple loss to bag loss in ducks shot at private hunting clubs and at public shooting grounds in Illinois, 1938-1945.

Place of Hunting	Year	Number Bagged	Number Crippled	Ratio of Cripple Loss to Bag Loss
Private hunting clubs-	1938	3,226	568	17.6:100
	1941	2,028	369	18.2:100
Public shooting grounds- - - - - - - -	1944	1,475	556	37.7:100
	1945	1,510	612	40.5:100

so severely wounded that they soon die. These two factors tend to counterbalance each other, and, in the absence of more detailed information, the cripple mortality rate used is that obtained by appraising the reports of hunters. The cripple loss of 9 per cent added to the proportion of mallards bagged, 32 per cent, brings the calculated total annual shooting losses of Mississippi flyway mallards up to 41 per cent of the population in the period 1939-1947.

The annual mortality rate of five year-classes of mallard drakes banded as adults at Lake Chautauqua averaged about 40 per cent, table 2. The year-of-banding mortality rate for males banded as juveniles was about 55 per cent, table 1. Since age ratios of male mallards in the Mississippi flyway, 1939-1947, show that juveniles comprise about half of the male fall population, then the annual mortality loss in the male population would be about 48 per cent. The mortalities in the female population and the entire population would be somewhat higher.

If shooting losses annually account for 41 per cent of the mallard population, and if the annual mortality is 48 per cent of this population, then natural losses would amount to only 7 per cent. Man is responsible for part of the losses usually classed as natural. Investigations on lead poisoning of ducks by James S. Jordan and the senior author, both of the Natural History Survey, tentatively indicate that annually 6 per cent of the mallard population in the Mississippi flyway die from this cause. Thus, man appears to be directly or indirectly responsible for most of the yearly mortality losses among Mississippi flyway mallards.

Our hunting-loss calculations have produced a maximum figure that is probably too high. An upward distortion in this figure could well have resulted from the high compensation figure (for non-report of bands) in deriving it.

The black duck has relatively lower hunting losses but higher total annual mortality rates than the mallard. Calculations based upon the same crippling rate and the same band-return rate for the black duck as for the mallard show that annual shooting losses for the black duck averaged about 34 per cent and natural losses about 20 per cent of this population.

From duck species that undergo above-average shooting losses, we turn for comparison of natural versus hunting losses in the blue-winged teal, a species that probably has smaller hunting losses than any other popular game duck.

Year-of-banding recoveries of blue-winged teals ranged from 1.4 to 3.6 per cent, table 12, and averaged about 2.45 per cent. Since many band recoveries from shot ducks come from south of the United States, where the incentive to turn in bands is probably not so great as in the United States, the proportion of bands not reported is probably higher in the blue-winged teal than in the mallard. However, lacking specific data, we have used the same correcting factor as was used for the mallard--190 per cent. This brings the yearly hunter-bag of blue-winged teals up to about 7 per cent of the total population of this species. The calculated cripple loss, 30 per cent of the number of blue-wings bagged, or 2 per cent of the total population, would increase the total annual shooting loss to 9 per cent.

The yearly mortality rates for the first 5 years following banding averaged about 57 per cent for blue-wings, table 7. The shooting mortality accounted for only 9 per cent of the population, leaving 48 per cent of the blue-wings' annual mortality to be accounted for by natural causes. Although the shooting mortality rate is considerably lower in the blue-wing than in the mallard, the over-all mortality rate is higher in the teal.

It seems significant that, although the shooting mortality rate is lower in the black duck and the blue-winged teal than in the mallard, the over-all mortality loss is greatest in the blue-winged teal, next so in the black duck, and least in the mallard. It is apparent that shooting losses do not account for all the differences in mortality rates among the three species of ducks.

Could the mallard ever have had an appreciably lower total mortality rate than it had for the period 1939-1947? No wild game bird species so far studied has such a low total mortality rate, even ring-necked pheasant populations, completely or partially protected. Song birds, much less productive than the mallard, have comparable annual mortality losses.

What has enabled the mallard to undergo heavy shooting losses without suffering higher over-all mortality rates?

Every wildlife population lives in an environment of limited carrying capacity. If hunters take the excess population, then the lower population density that results makes the remaining individuals less subject to predation, disease, food shortages, and other factors that contribute to natural losses.

It seems reasonable to us to assume that, in the mallard, heavy shooting losses have largely replaced natural losses that would otherwise have occurred to enable the population to live within the limitations of its environment. The mallard population has an internal elasticity that allows most of its components, including those that make up natural loss and shooting loss, considerable stretch or shrinkage. But the extent of stretch or shrinkage is limited, and the natural loss can never shrink to zero. Some natural loss must be expected, and the shooting loss cannot entirely replace the natural loss.

The conjecture that game bird populations possess internal elasticity is substantiated by Bump et al. (1947), who found that although hunting took 17 per cent of the ruffed grouse fall population in New York study areas, the gun increased the total mortality rate by only about 8

per cent, indicating that about half of the number of birds shot would have died before spring from natural causes, if the areas had not been opened to hunting.

In the 1939-1947 period, the natural loss in the mallard population migrating through Illinois was so small that any marked increase in the kill would undoubtedly have resulted in a proportionate rise in the total mortality. The natural loss had contracted to the point where a stretching of the hunting loss might have had disastrous results.

If this line of reasoning is valid, the blue-winged teal and perhaps the black duck could undergo greater hunting losses without raising their total mortality rates. In this connection, it is necessary to consider that the potential stretch and contraction, or "give and take," between natural mortality and shooting mortality differs in various species of ducks.

Several wild game species are known to possess a flexible productivity potential of such a nature that they respond to increased mortality with an increase in productivity.

Bump et al. (1947) found that, although hunting increased the mortality rate of ruffed grouse, the flexibility of the productivity potential tended to overcome this added loss. They found from a correlation of population data between protected and hunted populations that there was a distinct tendency for greater relative increases of young to be associated with lower breeding populations; thus, there was an inverse relationship between the number of grouse in the spring and the proportion of juveniles in the fall population. This population phenomenon has also been demonstrated by Errington (1945) to occur in bobwhites and by Allen (1943) in fox squirrels. Its wide occurrence in small game populations would lead us to suspect that it is present also in waterfowl populations.

To what extent the flexibility of the mallard's productivity potential could overcome increased mortality in Mississippi flyway populations is at present conjectural.

The mallard has a high reproductive potential and appears to be capable of maintaining its population under conditions of at least moderately high mortality losses. On the other hand, its breeding potential in the north may be affected by drastic annual fluctuations in breeding habitat, and in certain years, despite the excellent reproductive potential of this species, total numbers may be affected by the area available for expression of this potential.

This paper only opens the door to the subject of population losses in waterfowl. Even where the conclusions appear final, they may be only temporarily so. Future, more extensive studies may reveal, for example, that hunters report more or fewer bands, or that the loss from crippling is greater or less.

SUMMARY

1. This study of mallard, black duck, and blue-winged teal population losses in the Mississippi flyway is based on 10,718 of these ducks shot and recovered from 51,297 ducks banded at the Chautauqua National Wildlife Refuge or at McGinnis Slough in Illinois.

2. Because the banding of mallards and black ducks was done during the hunting season and about half way down the flyway, a correction of year-of-banding return data was made for these species so that the data would be comparable to the return figures in subsequent years. As most of the blue-winged teals were banded before the hunting season opened, no correction of year-of-banding returns was made for these ducks.

3. The mortality rate in a known age group, mallard drakes banded in the fall as juveniles, amounted to 55 out of 100 birds the first year, or year of banding, 20 the second year, 11 the third year, and 6 the fourth year. By the end of the sixth year, less than 3 of the original 100 were still alive.

4. The only marked differences in mortality rates among year-classes of mallards was between juveniles and adults. Mallard mortality was about 1-1/2 times as great for juvenile birds as for older ones; much of the difference resulted because juveniles are more vulnerable to shooting.

5. There was a higher mortality rate among mallard hens than among drakes. This higher rate apparently was not caused by hunting; it may have occurred because of natural disasters on the breeding grounds.

6. Of three species of ducks, mallard, black duck, and blue-winged teal, banded at McGinnis Slough, the mallard had the lowest mortality rate; it was followed in order by the black duck and the blue-winged teal.

7. The yearly hunter-bag rates followed a similar pattern for the three species. There was no consistent yearly trend in the hunter-bags, but the annual bag in the period 1944-1947 averaged about 1.5 per cent more per year than it did in the period 1940-1943.

8. Compared to other birds that have been studied for population mortality, mallards have a low rate of mortality. Although the blue-winged teal does not suffer the shooting losses that mallards do, its mortality rate is higher.

9. Band recovery data, corrected for proportion of bands unreported by hunters, and with estimated crippling losses included, indicate that hunters accounted for about 41 per cent of the 48 per cent annual mortality among Chautauqua-banded mallards, 1939-1947.

10. The high shooting-loss component in the mallard's annual mortality loss is indicative that, during the 1939-1947 period as a whole, the shooting losses probably absorbed a large part of the losses that would have been "natural" in an unshot population. However, because of the small part of the mortality loss left to be absorbed by natural losses, any marked increase in the shooting pressure over that occurring during the 1939-1947 period would undoubtedly have raised the mortality rate.

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